

Odonata biodiversity of the Argentine Chaco biome

Natalia von Ellenrieder

Instituto de Bio y Geociencias, Museo de Ciencias Naturales,
Universidad Nacional de Salta, Mendoza 2, Salta 4400, Argentina.
<natalia.ellenrieder@gmail.com>

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ABSTRACT

Odonates of small temporary pools, marshes, large permanent ponds, oxbow lakes, dams, and perennial rivers were sampled in the semiarid Chaco biome of NW Argentina between September 2007 and December 2008. Information from 35 localities yielded 60 species; presence/absence information of species was recorded in a spatial-relational database. Alpha, beta, and gamma diversity and total species richness expected for the area were estimated, and structure of Chaco odonate assemblages was preliminarily analyzed using nonmetric multidimensional scaling (NMS) ordination. Species composition was found to be related to both habitat type and longitudinal sector. Some species that might be indicative of habitat type were identified. — In order to analyze the distribution and biogeography of the odonates of the Chaco biome in Argentina, collections and literature were also examined, adding 58 localities (93 total) and 28 species (88 total). Odonate diversity of the Chaco was compared with that of neighboring Yungas and Paranense biomes by means of percent complementarity and cluster analysis, which showed Chaco odonate composition to be slightly more similar to that of the Yungas than to the Paranense biome, and W and E Chaco sectors to be more similar between them than with either of the two neighboring biomes. Most odonate species found in the Chaco are vagile and more widely distributed in the Neotropical region, with only four potential endemics.

RESUMEN

Se muestrearon Odonatos de pequeños charcos temporarios, esteros, grandes lagunas, madrejones, diques y ríos en el NO de Argentina entre septiembre de 2007 y diciembre de 2008. Datos de presencia/ausencia de especies se registraron en una base de datos espacio-relacional. Información de 35 localidades proporcionó un total de 60 especies. Se estimaron la diversidad alfa, beta y gama, y la riqueza de especies esperada para el área, y un análisis preliminar de la estructura de asociaciones de odonatos del Chaco

fue realizado mediante ordenamiento multidimensional no-métrico (NMS). La composición de especies se encontró relacionada con el tipo de hábitat y sector longitudinal. Se identificaron algunas especies con valor potencial como indicadores de tipo de hábitat. — Con el fin de analizar la distribución y biogeografía de los odonatos del bioma de Chaco en Argentina, se examinaron además colecciones y literatura, agregando 58 localidades (total de 93) y 28 especies (total de 88). Se comparó la composición de odonatos del Chaco con la de los biomas colindantes de las Yungas y Paranense mediante porcentaje de complementariedad y análisis de agrupamientos, mostrando que la composición de odonatos del Chaco es ligeramente más similar a la del bioma de las Yungas que al Paranense, y que los sectores O y E del Chaco son más similares entre sí que con cualquiera de los dos biomas adyacentes. Casi todas las especies de odonatos halladas en el Chaco son vágiles y se encuentran más ampliamente distribuidas en la región Neotropical, con solo cuatro potenciales endemismos.

INTRODUCTION

Odonates have been proposed as suitable indicators of the health or integrity of freshwater wetlands (Moore 1984; Clausnitzer 2004; Kalkman et al. 2008). Their larvae are sensitive to water quality and aquatic habitat morphology given by bottom substrate and aquatic vegetation structure, while habitat selection of their adults is based mainly on vegetation structure, showing strong responses to habitat change such as thinning of forest and increased erosion (Clark & Samways 1996; Stewart & Samways 1998; Sahlén & Ekestubbe 2001). Baseline knowledge of assemblages and habitat preferences of odonates is a prerequisite to use them as indicators of habitat alteration and monitor conservation and restoration of wetlands (Corbet 1993). Several studies have characterized odonate communities and species richness in relation to habitat in tropical areas of Africa (Clausnitzer 2003; Dijkstra & Lempert 2003; Suhling et al. 2006), Indonesia (Cleary et al. 2004), Malaysia (Furtado 1969), Mexico (Novelo-Gutiérrez & Gómez-Anaya 2009), Colombia (Pérez et al. 2007), Surinam (Wasscher 1993), and Peru (Louton et al. 1996) but such knowledge is still nonexistent for the South American Chaco.

Biodiversity of the Chaco is the third in importance in Argentina after that of the Paranense and Yungas forests (based mostly on plant and vertebrate censuses, Bertonatti & Corcuera 2000). Odonates of this biome are known only from fragmentary records represented by studies referring to a particular locality (National Park Mburucuyá in Muzón et al. 2008) or particular taxa (e.g. von Ellenrieder 2008; von Ellenrieder & Garrison 2008). The provinces of Formosa and Chaco, entirely included within the Chaco biome in Argentina, are poorly known; 26 species have been recorded from Formosa and 27 for Chaco, in strong contrast with the adjacent provinces of Salta and Corrientes, for which 100 and 92 species respectively are known (von Ellenrieder & Muzón 2008). Even though odo-

nate biodiversity in the Yungas and Paranense forests within Salta and Corrientes provinces is considered as relatively well known (von Ellenrieder & Garrison 2007; Muzón et al. 2008; von Ellenrieder 2009a), such is not the case for the semiarid areas of Chaco that these provinces include.

The goals of this study were to provide a first inventory of the odonates of the Argentine Chaco, perform a preliminary analysis of the alpha, beta, and gamma diversity of their assemblages, explore their potential for indicator species of different habitats, and compare their composition with that of assemblages from the neighboring Yungas and Paranense biomes.

MATERIAL AND METHODS

Study area

The Chaco biome corresponds to a biogeographical province extending across N Argentina, NW Paraguay, SE Bolivia, and a narrow stripe along Mato Grosso do Sul State in SW Brazil (Cabrera & Willink 1973; Morrone 2001). Landscape is approximately flat, with a slight declination towards the east. Geologically the Chaco plains correspond to a tectonic depression filled with 3,000 m of sediments dating from the Paleozoic, Mesozoic, and Tertiary, covered with fine non-consolidated Quaternary sediments. Soils are usually neutral or slightly alkaline, with a high base level of saturation (90-100%). To the west, soils can be acidic and are more open and sandy with good drainage; in the east they are rich in clay and have poor drainage. Due to the semiarid climate, primary minerals and soluble salts are abundant and result in areas of salty soils. Eighty percent of the region is included in the Río de La Plata watershed, and its main tributaries crossing the Chaco are the rivers Pilcomayo, Bermejo, and Juramento-Salado. In dry areas rivers are ephemeral and change their course year to year; in wet areas they are permanent. Summers are hot and humid, and winters temperate with occasional frost, becoming dryer due to decrease in precipitation toward the west (Prado 1993). During the irregular rainy season from October to April there is flooding which can cover up to 15% of the territory for several months. Based on climatic conditions, two broad zones have been recognized (Burkart et al. 1994): (1) Eastern Chaco, humid to sub-humid with 1,250 mm of rain per year in the E and 750 mm in the W, and an mean yearly temperature of 23°C; (2) Western Chaco, semi-arid to arid, with 750–350 mm of rain per year from east to west and with an mean yearly temperature of 28°C. Botanically the Chaco is defined by the presence of the Quebracho Colorado tree (*Schinopsis balansae*). Although the predominant vegetation is a deciduous xerophytic forest with species in three to four strata, comprising a stratum of trees, one of shrubs, one of grasses, or cacti, and some-

times one of terrestrial bromeliads, it constitutes a heterogeneous mosaic of different habitats. Localized conditions of soil and weather lead to the development of gallery forests along rivers – which may or may not flood yearly – wetlands, palm forests, savannas, grasslands, halophytic shrub-steppes, and cacti zones (Cabrera & Willink 1973; Ramella & Spichiger 1989).

Sampling and data recording

Odonates were sampled at 35 localities representing major types of freshwater habitats in the study area, including temporary rain pools and artificial water holes, marshes, large impoundments, and perennial rivers, from protected and non-protected areas within the Chaco biome in Salta and Formosa provinces, NW Argentina (Table 1, Fig. 1). Each locality was visited one to three times between September 2007 and December 2008, several being dry in subsequent visits (for effective number of sampling visits see Table 1). Because the knowledge of the larval stage of the odonates of the area is still incomplete, species lists were based on representative qualitative samples of adults only, collected with an aerial net. Presence/absence information of species was recorded into a spatial-relational database. Localities were classified according to longitudinal sector and habitat type. Sectors correspond to the arid Western Chaco and sub-humid Eastern Chaco (Burkart et al. 1994), with their limit in Argentina along an approximately straight line running from 59°W in Formosa Province to 61°W in Santa Fe Province (Fig. 1). All environments were open habitats well exposed to the sun. They were classified into:

- large permanent lentic environments: including large ponds, oxbow lakes, and dams, usually provided with floating and riparian vegetation;
- small temporary lentic environments: including rain pools, artificial water holes, and small ponds, with water only after rainy season (between November and May in dry Western sector), aquatic vegetation sparse or absent, and shores generally bare due to varying water levels or grazing cattle;
- marshes: shallow water, well vegetated with various submerged plants and reeds;
- lotic, perennial rivers: with vegetation along banks, including shrubs and trees.

Examination of collections (Fundación e Instituto Miguel Lillo, Tucumán, Argentina; Museo de La Plata, La Plata, Argentina; personal collection of R.W. Garrison, Sacramento, California, USA) and literature (Martin 1908; Calvert 1909, 1956; Ris 1911, 1913, 1919, 1928; Navás 1920, 1922, 1927, 1928; Fraser 1947, 1948; Gloger 1967; Belle 1970; Bulla 1970, 1971; Rodrigues Capítulo & Muzón 1989) yielded additional localities and species that were included in the analysis of the distribution and biogeography of Chaco odonates.

Table 1. Localities with odonate records from the Argentine Chaco; protected areas indicated with an asterisk. For field data habitat type (Ha) is indicated as LeT: small lentic temporary; LeM: marsh; LeP: large lentic permanent; Lo: Lotic. W: Western Chaco; E: Eastern Chaco; LC: literature and collections; FD: field data, number of sampling visits is indicated in parenthesis; S: species richness.

Code	Province, locality	Altitude	Coordinates	Ha	Sector	Source	S
Cb1	Córdoba, Cabaña	729	31.2167°S, 64.3667°W		W	LC	1
Cb2	Córdoba, Capilla del Monte	972	30.8500°S, 64.5167°W		W	LC	1
Cb3	Córdoba, Huerta Grande	963	31.0667°S, 64.5000°W		W	LC	1
Cb4	Córdoba, La Calera	469	31.3333°S, 64.3333°W		W	LC	2
Cb5	Córdoba, Salsipuedes	744	31.1500°S, 64.3167°W		W	LC	3
Co1	Corrientes, Corrientes	51	27.4667°S, 58.8333°W		E	LC	17
Co2	Corrientes, Goya	24	29.1333°S, 59.2667°W		E	LC	5
Co3	Corrientes, Itatí	67	27.2667°S, 58.2500°W		E	LC	1
Co4	Corrientes, Manantiales	60	27.9500°S, 58.1333°W		E	LC	11
Co5	Corrientes, Parque Nacional Mburucuyá*	70	28.0500°S, 58.2333°W		E	LC	18
Co6	Corrientes, Paso de la Patria	50	27.3167°S, 58.5833°W		E	LC	5
Co7	Corrientes, San Cosme	63	27.3667°S, 58.5167°W		E	LC	6
Co8	Corrientes, San Diego	64	28.7500°S, 58.6500°W		E	LC	1
Co9	Corrientes, San Roque	70	28.5667°S, 58.7167°W		E	LC	2
Co10	Corrientes, Santa Ana	62	27.4500°S, 58.6667°W		E	LC	2
Ch1	Chaco, Ciervo Petiso	72	26.5833°S, 59.6333°W		E	LC	1
Ch2	Chaco, Colonia Benítez	54	27.3333°S, 58.9333°W		E	LC	8
Ch3	Chaco, Machagai	74	26.9333°S, 60.0500°W		E	LC	1
Ch4	Chaco, Presidencia Roque Sáenz Peña	90	26.7833°S, 60.4500°W		W	LC	5
Ch5	Chaco, Puerto Bermejo	44	26.9333°S, 58.5000°W		W	LC	18
Ch6	Chaco, Quitilipi	81	26.8667°S, 60.2167°W		E	LC	2
Ch7	Chaco, Resistencia	47	27.4500°S, 58.9833°W		E	LC	7
Ch8	Chaco, Pozo de La Gringa	132	25.3244°S, 60.9892°W		E	LC	1
Fo1	Formosa, Bañado La Estrella	61	24.4589°S, 60.3881°W	LeP	W	FD(2)	18
Fo2	Formosa, Bartolomé de las Casas	80	25.4000°S, 59.5667°W		E	LC	1
Fo3	Formosa, Clorinda	60	25.2833°S, 57.7167°W		E	LC	8
Fo4	Formosa, ditch by road (2)	63	25.9850°S, 58.0383°W	LeM	E	FD	10
Fo5	Formosa, Espinillo	72	24.9667°S, 58.5667°W		E	LC	2
Fo6	Formosa, Estancia Guaycolec	185	25.9833°S, 58.2000°W		E	LC	3
Fo7	Formosa, Formosa	56	26.1833°S, 58.1833°W		E	LC	3
Fo8	Formosa, Gran Guardia	65	25.8667°S, 58.8833°W		E	LC	1
Fo9	Formosa, NE of Formosa	185	25.9833°S, 58.2000°W		E	LC	1
Fo10	Formosa, P.N. Pilcomayo, Laguna Blanca*	74	25.1747°S, 58.1289°W	LeP	E	FD(1)	16

Code	Province, locality	Altitude	Coordinates	Ha	Sector	Source	S
Fo11	Formosa, P.N. Pilcomayo, Estero Catalina*	72	25.1092°S, 58.1533°W	LeM	E	FD(1)	8
Fo12	Formosa, 12 km of Gran Guardia	62	25.9650°S, 58.9292°W	LeT	E	FD(1)	12
Fo13	Formosa, Puesto Porteño	110	24.7167°S, 59.5833°W		W	LC	2
Fo14	Formosa, N of Las Lomitas	120	24.5583°S, 60.4686°W	LeT	W	FD(2)	7
Fo15	Formosa, Reserva Natural Formosa*	122	24.3167°S, 61.7978°W	LeP	W	FD(1)	12
Fo16	Formosa, Riacho He He	77	25.4950°S, 57.8367°W	Lo	E	FD(1)	1
Fo17	Formosa, N of Mojón de Fierro	48	26.0219°S, 58.0447°W	LeT	E	FD(1)	7
Fo18	Formosa, S of Mojón de Fierro	47	26.0492°S, 58.0667°W	LeT	E	FD(1)	13
Fo19	Formosa, 40 km W of Formosa	52	25.9464°S, 58.4950°W	LeT	E	FD(1)	5
Fo20	Formosa, 48 km W of Formosa	51	25.9122°S, 58.5681°W	LeT	E	FD(1)	6
Fo22	Formosa, E of Juárez	153	23.9706°S, 61.7039°W	LeT	W	FD(2)	10
Fo24	Formosa, Laguna Yema	156	24.3508°S, 61.3147°W	LeP	W	FD(2)	5
Fo25	Formosa, 5.2 km NW of Ingeniero Juárez	185	23.8767°S, 61.8989°W	LeT	W	FD(1)	3
Fo26	Formosa, PR 512 km NW of Ingeniero Juarez	190	23.8450°S, 61.9631°W	LeT	W	FD(2)	10
Sa1	Salta, Aguaray	568	22.2667°S, 63.7333°W		W	LC	4
Sa2	Salta, Joaquín V. González	366	25.0833°S, 64.1833°W		W	LC	2
Sa3	Salta, Salta Forestal	649	24.9167°S, 64.4667°W		W	LC	16
Sa4	Salta, Apolinario Saravia	360	24.4378°S, 63.9717°W	LeT	W	FD(1)	8
Sa5	Salta, Campo Durán	558	22.2333°S, 63.7000°W		W	LC	1
Sa6	Salta, Dique El Tunal	566	25.2194°S, 64.4867°W	LeP	W	FD(2)	21
Sa7	Salta, Embarcación	273	23.2167°S, 64.1000°W		W	LC	2
Sa8	Salta, NR 81 km 327 N of Dragones	270	23.1733°S, 63.6628°W	LeT	W	FD(2)	5
Sa9	Salta, Salta, Laguna 2 km Acceso N	1256	24.7628°S, 65.3161°W	LeT	W	FD(1)	5
Sa10	Salta, Las Lajitas	499	24.7400°S, 64.2017°W	LeT	W	FD(2)	7
Sa11	Salta, Lumbreras, Río Juramento	645	25.1850°S, 64.9167°W		W	LC	3
Sa12	Salta, Morenillo	864	26.2000°S, 64.8500°W		W	LC	1
Sa13	Salta, NR 81, ponds with riparian vegetation	240	23.4519°S, 62.9319°W	LeT	W	FD(1)	8
Sa14	Salta, NR 81 ponds with <i>Pistia</i>	225	23.5203°S, 62.7819°W	LeT	W	FD(1)	6
Sa15	Salta, pond 1 km E Embarcación	392	23.2050°S, 64.0789°W	LeT	W	FD(3)	19
Sa16	Salta, PR 15, W of Las Varas	392	23.3553°S, 64.1436°W	LeT	W	FD(2)	6
Sa17	Salta, NR 81, <i>Azolla</i> ponds	533	25.3908°S, 64.6381°W	LeT	W	FD(1)	1
Sa18	Salta, Río del Valle Dorado	467	24.7033°S, 64.1886°W	Lo	W	FD(1)	1
Sa19	Salta, NR 81, W of Dragones	328	23.1142°S, 63.7783°W	LeT	W	FD(1)	2
Sa21	Salta, slough by PR 5	439	24.7033°S, 64.1283°W	LeT	W	FD(1)	5

Code	Province, locality	Altitude	Coordinates	Ha	Sector	Source	S
Sa22	Salta, dark water slough by PR 5	385	24.4981°S, 64.0392°W	LeT	W	FD(1)	4
Sa23	Salta, Embalse Cabra Corral	1050	25.2956°S, 65.3517°W		W	LC	7
Sa24	Salta, pond 1.5 km E of Embarcación	281	23.2056°S, 64.0694°W	LeT	W	FD(2)	20
Sa25	Salta, dam 17.5 km E of Embarcación	278	23.2186°S, 63.9153°W	LeT	W	FD(1)	3
Sa26	Salta, pond 1 km NW Teniente General Fraga	198	23.7472°S, 62.1614°W	LeT	W	FD(1)	6
Sa27	Salta, El Gallinato, stream	1256	24.6794°S, 65.3408°W	Lo	W	FD(1)	4
Sa28	Salta, La Viña	1265	25.4333°S, 65.5833°W		W	LC	1
Sa29	Salta, stream by PR 5	332	23.4736°S, 64.1247°W	Lo	W	FD(1)	1
Sa30	Salta, Salta Forestal, ponds	649	24.9167°S, 64.4667°W		W	LC	20
Sa31	Salta, Joaquín V. González, Río Juramento	402	25.1089°S, 64.1850°W		W	LC	6
SF1	Santa Fe, Ruta 34, 2 km N of Hersilia	180	29.9619°S, 61.8717°W		E	LC	1
SF2	Santa Fe, Villa Ana	49	28.4833°S, 59.6167°W		E	LC	5
SF3	Santa Fe, Villa Guillermina	39	28.2333°S, 59.4667°W		W	LC	1
SE1	Santiago del Estero, 14 km S of Antilla	352	26.2833°S, 64.4667°W		W	LC	1
SE2	Santiago del Estero, Añatuya	98	28.4667°S, 62.8333°W		W	LC	4
SE3	Santiago del Estero, Colonia Dora	101	28.6000°S, 62.9500°W		W	LC	5
SE4	Santiago del Estero, Chaco, Mistol	87	28.6833°S, 62.9000°W		W	LC	7
SE5	Santiago del Estero, Aguirre	97	29.3500°S, 62.4500°W		W	LC	1
SE6	Santiago del Estero, Icaño	87	28.6833°S, 62.9000°W		W	LC	5
SE7	Santiago del Estero, Termas de Río Hondo	248	27.5253°S, 64.9456°W		W	LC	16
SE8	Santiago del Estero, Río Salado	119	27.9333°S, 63.4500°W		W	LC	1
SE9	Santiago del Estero, Santiago	181	27.7833°S, 64.2667°W		W	LC	2
Tu1	Tucumán, Chilcas	494	26.3667°S, 64.6833°W		W	LC	1
Tu2	Tucumán, Las Cejas	313	26.8833°S, 64.7333°W		W	LC	3
Tu3	Tucumán, Garmendia	345	26.5667°S, 64.5500°W		W	LC	1
Tu4	Tucumán, Monte Bello	294	27.2333°S, 65.1167°W		W	LC	3

Data analysis

Richness

Based on the field data three diversity indices were estimated as defined by Whittaker (McCune et al. 1997): alpha diversity, calculated as the mean specific richness

per locality; beta diversity, a measurement of the heterogeneity of the data, calculated as the ratio between total number of species and mean number of species; and gamma diversity, or diversity at landscape level, calculated as total number of

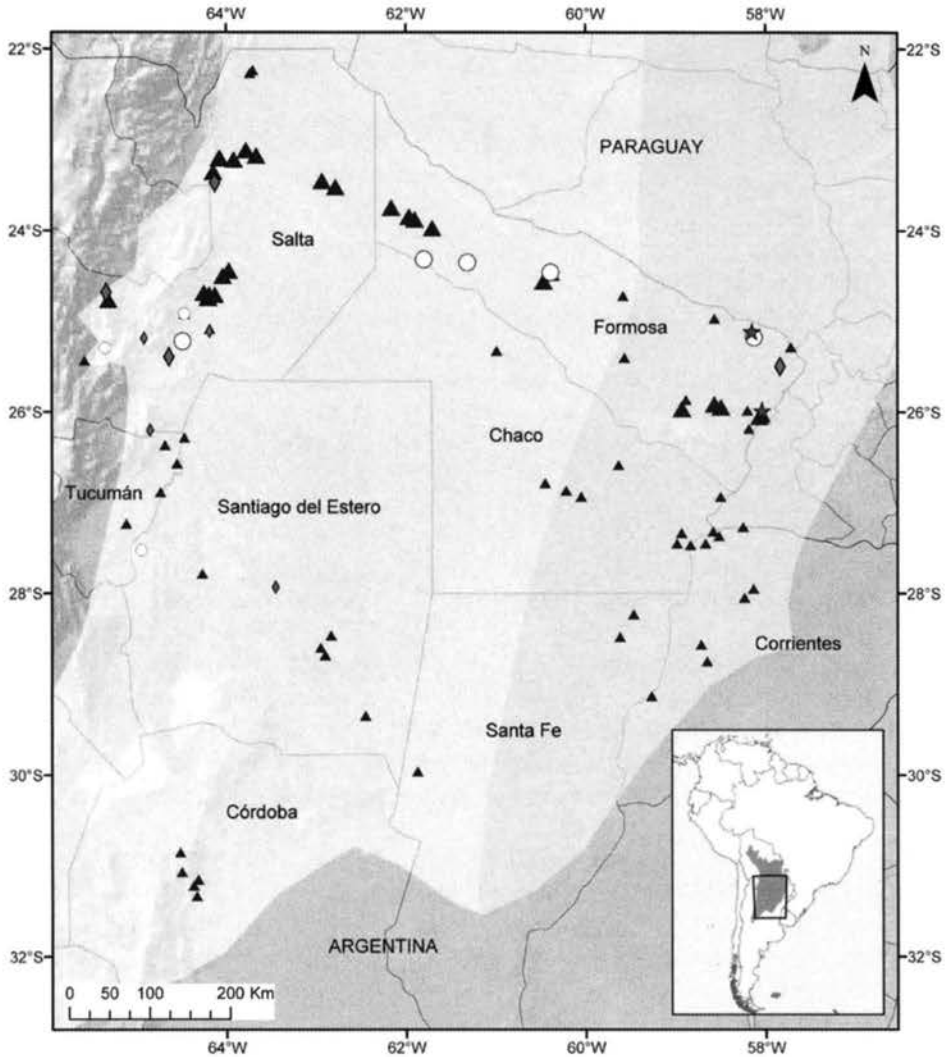


Figure 1: Map of NW Argentina showing localities studied in the Chaco biome (only Provinces with data are labeled). Shaded: Chaco biome; lighter shading on left: W Chaco, darker shading on right: E Chaco. Shapes indicate habitat type and size source of data: \blacktriangle small lentic temporary; \star marsh; \bigcirc large lentic permanent; \blacklozenge lotic; large size: field data; small size: data from collections and literature. Inset map shows extension of Chaco biome in South America.

species across all localities. Expected species richness was calculated with the first and second order Jackknife and Chao 2 non-parametric estimators.

Structure

A preliminary analysis of the patterns of species composition was performed by means of ordination analysis using nonmetric multidimensional scaling (NMS; Mather 1976) run with the program PC-ORD (McCune & Grace 2002). This ordination method was chosen because it is suitable for heterogeneous data, i.e. on arbitrary or discontinuous scales or based on data sets with numerous zero values, e.g. presence-absence matrices, and because it can extract information from nonlinear relationships. Sorensen was chosen as distance coefficient. Forty runs were carried out with real data and 50 with random data (Monte Carlo test) starting from a random configuration, and with a possible maximum of six axes and 400 iterations. Final instability was calculated as standard deviation in stress over the preceding 15 iterations (value $< 10^{-4}$ indicates a stable solution; McCune & Grace 2002). Proportion of variance represented by ordination axes was calculated by correlation (determination coefficient r^2) between Euclidean distances in ordination space and distances in original space. Distances in original space were calculated with the same distance measure used in NMS analysis. Longitude, latitude, altitude, and habitat type for each locality were included in an environmental matrix, then transformed into ordinal variables, correlated with NMS ordination axes, and overlaid onto the ordination diagrams as joint plots, where angle and length of radiating lines indicate direction and strength of relationships between variables and ordination axis. Only variables from the environmental matrix with an $r^2 > 0.20$ were represented. Groups defined by habitat type and sector were overlaid onto the NMS ordination to aid in the interpretation of their relationships.

Groups defined by habitat type and longitudinal sector were compared by means of multiple response permutation procedure (MRPP) tests to see if they differed significantly in their odonate composition. This method provides a multivariate non-parametric test of differences among two or more groups based on the analysis of a distance matrix. Sorensen was used as distance coefficient. Delta (mean weighted distance within a group; lower delta value indicates better cohesion within a group) was calculated according to the procedure detailed by Mielke & Berry (2001). The statistic of this method, $T = \text{observed-expected delta} / \sqrt{\text{variance of delta}}$, describes separation between groups (the more negative the value of T , the larger the separation between groups), A describes homogeneity within each group compared to one due to chance, and p represents the probability of obtaining a delta as high as or higher than observed by chance given the distribution.

Indicator species

Indicator species analysis calculated with the method described by Dufrêne & Legendre (1997) was performed to identify potential indicators for the groups defined by habitat type. This method combines information about relative species abundance and frequency of occurrence in each group. A perfect indicator for a particular group (indicator value of 100) must be faithful (always present) and exclusive to the group (never occurring in other groups). Statistical significance of the indicator values was established with a Monte Carlo test (with 1,000 permutations).

Distribution and biogeography

Odonate composition of the Chaco was compared with that of neighboring Yungas and Paranense biomes (Fig. 2). Distribution data of odonates in the Yungas

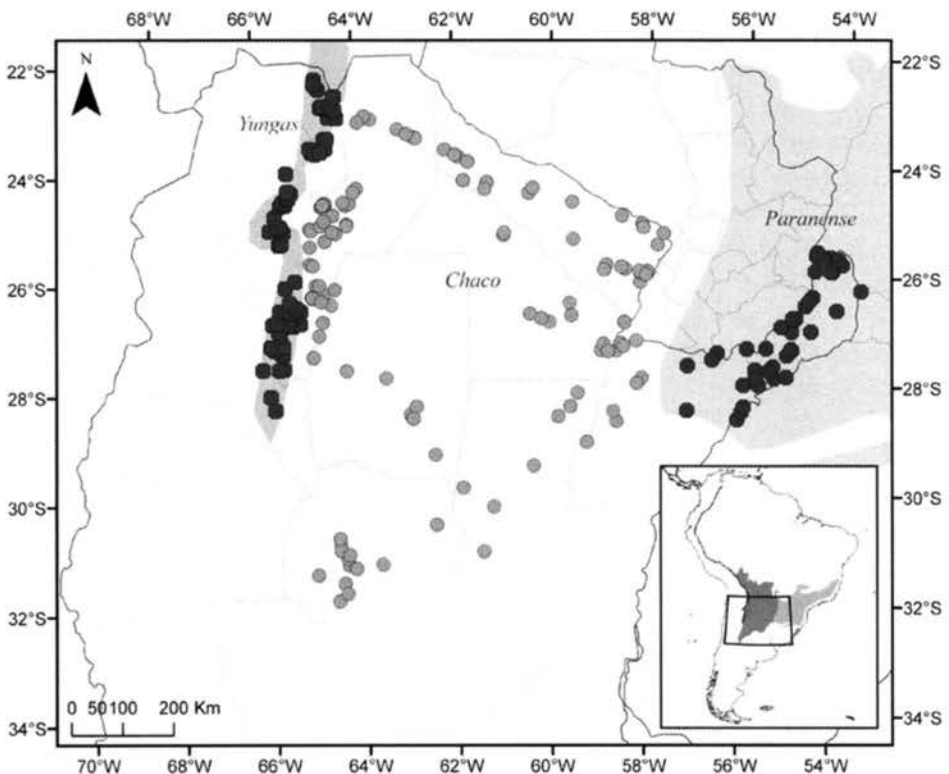


Figure 2: Map of NW Argentina showing localities of Yungas, Chaco, and Paranense biomes in Argentina included in this study. Inset map shows extension of the three biomes in South America.

were taken from von Ellenrieder (2009a) and updated with recent field data; data for Paranense biome from Paranense localities in Muzón et al. (2008) and von Ellenrieder & Muzón (2008) complemented with collection data (all data are available from the author at request). Percentage complementarity, a measurement of distinctness or dissimilarity (Colwell & Coddington 1994), was calculated among the three biomes and between both Chaco sectors, and a multivariate cluster analysis among them was performed using Sorensen (Bray-Curtis) as distance coefficient, and flexible Beta with a value of $\beta = -0.25$ as linkage method. The resulting dendrogram was based on Wishart's objective function converted to a percentage of remaining information (McCune & Grace 2002).

RESULTS

Richness

The 35 localities sampled (Table 1) along a W to E transect in Salta and Formosa provinces (Fig. 1), resulted in 60 species (gamma diversity) belonging to 28 genera and six families (Appendix). Species richness per locality varied from 1 to 21 (Table 1), with a mean (alpha diversity) of 7.85. Beta diversity was 7.64. Most widespread species (recorded from 14 or more localities) were *Ischnura fluviatilis*, *Telebasis willinki* (Coenagrionidae), *Miathyria marcella*, *Micrathyria longifasciata*, and *Orthemis nodiplaga* (Libellulidae); 21 species were found at only one locality, and nine at only two. Four species were first records for the country, three of which were new to science; one species of Coenagrionidae: *Telebasis* sp. nov. 2, three Libellulidae: *Erythemis carmelita*, *Oligoclada* sp. nov. (already described as *O. rubribasalis*; Appendix), and *Orthemis* sp. nov. (already described as *O. philipi*; Appendix), and 27 species constituted first records for four provinces (Appendix). Small lentic temporary water bodies presented between 1 and 20 species per locality ($n = 24$, mean 7.29, s.d. 4.72), marshes 8 to 10 ($n = 2$, mean 9.0, s.d. 1), large lentic permanent waters 5 to 21 ($n = 5$, mean 14.20, s.d. 5.49), and lotic environments 1 to 4 ($n = 4$, mean 2.4, s.d. 1.29). Estimates for total number of species to be expected in the sampled area were of 80.4 (first-order jackknife), 84.5 (Chao 2), and 92 (second-order jackknife).

Examination of collections and literature yielded another 28 species, adding to a total of 88 species in 41 genera (Appendix; Fig. 5) and 93 localities across the entire extension of the Chaco in Argentina (Table 1; Fig. 1). Best represented family was Libellulidae with 51 species, followed by Coenagrionidae with 23 species. The richest genus was *Erythrodiplex* with 12 species, followed by *Erythemis*, *Micrathyria*, and *Telebasis* with five species each. One species was first record for the country, *Telebasis* sp. nov. 1, and four species constituted first records for two provinces (Appendix). W and E Chaco sectors shared 45.45% of their species, accounting for 72 and 54 species respectively (Appendix).

Structure

NMS analysis resulted in a three dimensional solution after 318 iterations with a final stress of 17.13, final instability of 10^{-6} , and a proportion of randomized runs with stress lower than or equal to observed stress of 0.0196. Variance represented by the three ordination axes was of 19.0%, 36.6%, and 22.1% respectively (cumulative variance of 77.7%). Longitude, latitude, and altitude were significantly correlated to ordination axis 3 while habitat type explained community composition along axis 2 (Table 2). This was evident in the ordination diagram, where the assemblages from western and eastern sectors (Figs 3b, c) and from lentic and lotic environments (Figs 3a, b) were clearly separated.

Comparison among groups defined by habitat type and sector by means of MRPP tests confirmed that their differences in composition were statistically significant (Table 3).

Table 2. NMS analysis: Pearson and Kendall Correlations of locality variables with ordination axes. Variables with an r^2 larger than 0.20 shown in joint plots of Figure 3 are highlighted in bold. Categorical variable for habitat type was transformed into an ordinal variable as $n-1$.

Variables	Axis 1			Axis 2			Axis 3		
	r	r^2	τ	r	r^2	τ	r	r^2	τ
Altitude	0.422	0.178	0.251	0.324	0.105	-0.032	-0.543	0.295	-0.591
Latitude	-0.066	0.004	-0.061	-0.218	0.048	-0.246	-0.498	0.248	-0.272
Longitude	-0.216	0.047	-0.166	0.029	0.001	0.035	0.857	0.735	0.657
Habitat type	-0.112	0.013	-0.159	0.718	0.515	0.453	-0.153	0.023	-0.093

Indicator species

Indicator analysis identified some species with a significant indicator value for large permanent lentic environments and for marshes. No perfect indicator was found, and only a few species had a relatively high indicator value which could be considered biologically meaningful (highlighted in Table 4).

Distribution and biogeography

Only 12 of the recorded species from the Chaco were not shared with neighboring biomes while 76 species were shared with either Yungas (11) or Paranense (24) biomes or with both (35). Diversity of Chaco odonates was found to be much lower than that of adjacent Yungas and Paranense biomes in Argentina. As in the other two biomes, Libellulidae followed by Coenagrionidae were the richest fami-

lies, but several families were absent and generic and species richness were lower for most of the families shared (Fig. 4). Percent complementarity values showed Chaco assemblages to be slightly more similar to assemblages of the Yungas than to those of the Paranense biome. Both percent complementarity (Table 5) and cluster analysis (Fig. 5) showed that assemblages from E and W Chaco are more similar among themselves than with either one of the other two biomes.

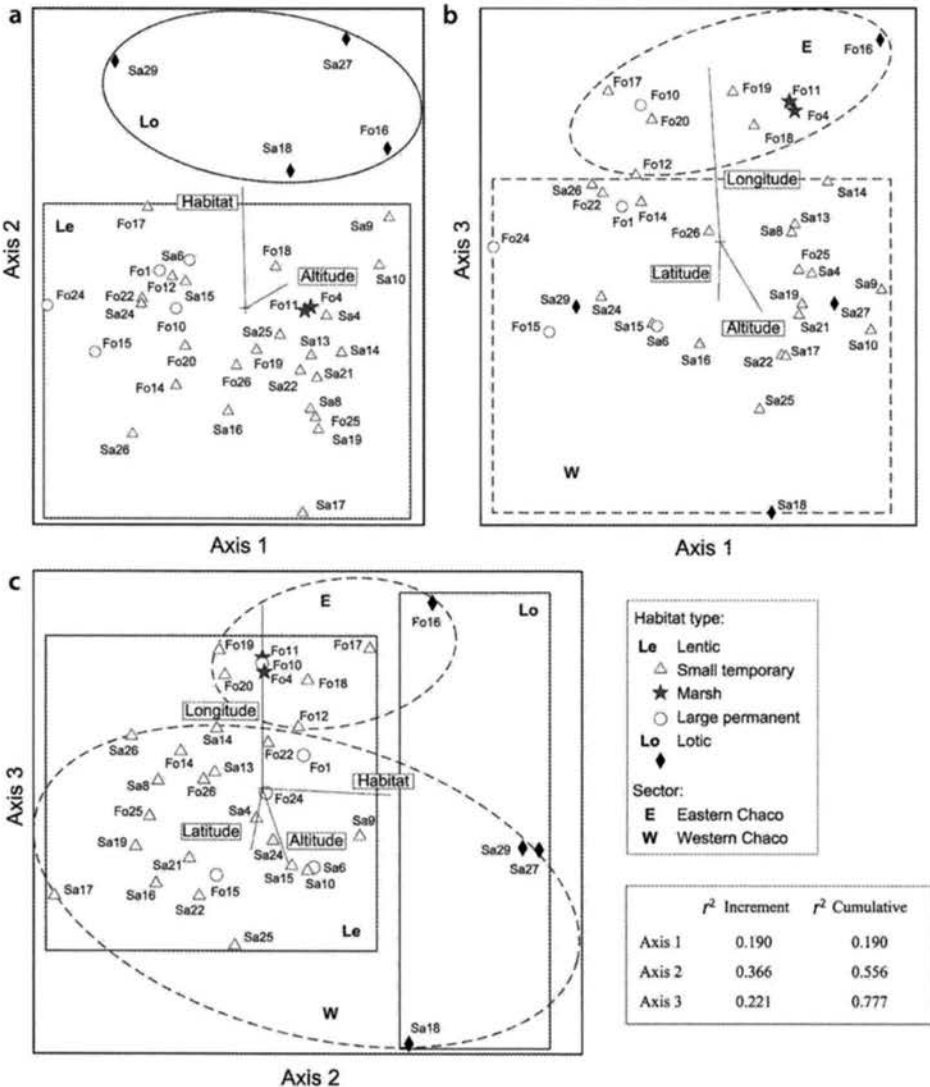


Figure 3: Joint plots showing relationship among environmental variables and axes 1 to 3 from NMS ordination of odonate assemblages of Argentine Chaco: (a) axes 1 and 2; (b) axes 1 and 3; (c) axes 2 and 3.

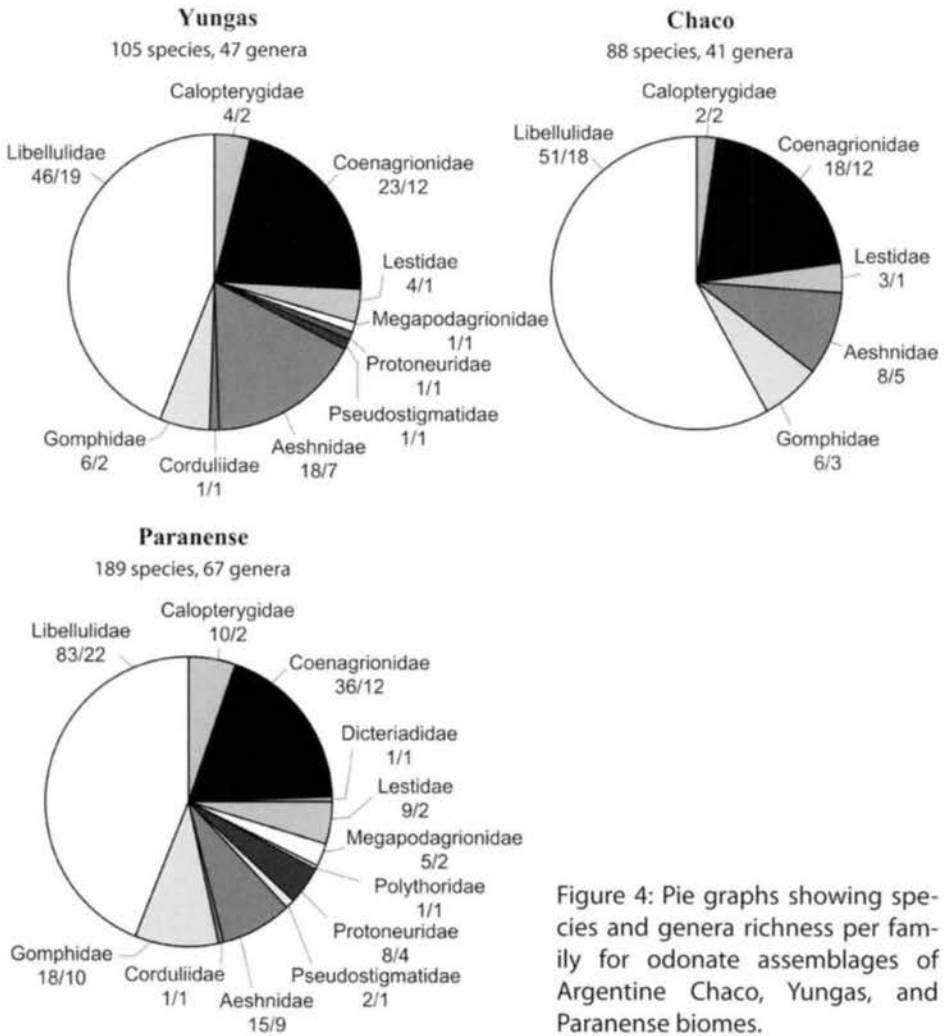


Figure 4: Pie graphs showing species and genera richness per family for odonate assemblages of Argentine Chaco, Yungas, and Paranense biomes.

DISCUSSION

Community analysis

The number of odonate species found in the northern portion of the Chaco in Argentina, 60 from field samples plus nine from other collections realized from within the same area, represents 75-85.8% of the expected species richness for this area according to the theoretical estimates. Novelo-Gutiérrez & Gómez-Anaya (2008) tested the efficiency of different predictors and found Chao 2 to provide the best approximation for total species richness in odonate assemblages from Mexico. According to the Chao 2 estimate obtained here, about 15 more species

Table 3. Results of MRPP test comparing groups defined by habitat type and longitudinal sector. *T*: observed-expected delta/ $\sqrt{\text{variance of delta}}$; describes separation between the groups; the more negative the value of *T* the larger the separation between the groups. Delta: mean inner distance within a group (lower delta indicates better cohesion within the group). *p*: probability of obtaining a delta as high as or higher than observed given the distribution of possible deltas (probability that observed difference is due to chance). *A*: describes homogeneity within each group compared to one due to chance, with *A* = 1, when all items are identical within the group; *A* = 0, when heterogeneity within groups equals expectation by chance; *A* < 0, with more heterogeneity within groups than expected by chance.

	Mean inner distance	<i>A</i>	<i>T</i>	Observed delta	Expected delta	Variance of delta	<i>p</i>
Habitat	–	0.10	-7.00	0.68	0.77	0.13	0.02 ⁻⁵
Lentic marsh (n 2)	0.11	–	–	–	–	–	–
Lentic permanent (n 5)	0.60	–	–	–	–	–	–
Lentic temporary (n 24)	0.69	–	–	–	–	–	–
Lotic (n 4)	1.00	–	–	–	–	–	–
Sector	–	0.062	-8.16	0.72	0.76	0.34	0.12 ⁻⁵
Eastern (n 9)	0.62	–	–	–	–	–	–
Western (n 26)	0.75	–	–	–	–	–	–

could be expected in this portion of the Chaco. Central and southern portions of this biome in Argentina have scarcely been sampled for odonates, with relatively broad areas still unexplored (Fig. 1, Appendix). The early stage of our knowledge of this fauna is also evidenced by discovery of four new species in a period of slightly over one year of fieldwork, and by our incomplete knowledge of their biology, with larval stage of ca a third (32%) of the recorded species still unknown.

According to the preliminary analysis of the structure of Chaco communities performed here, the combined effect of habitat type and climatic longitudinal gradient of dry western to sub-humid eastern Chaco is reflected in the composition of odonate assemblages, both explaining almost 60% of the variance (Fig. 3c). These results need to be tested by further sampling, as local communities were analyzed based on one or a few adult samples only and, especially for permanent waters, will therefore not include a complete representation of the species characteristic of each habitat type. Unmeasured factors acting upon the community that might explain the unaccounted variance along axis 1 could include structure of larval habitat, abiotic factors such as salinity, pH, size, depth, and temperature of the water body (Peckarsky 1983; Corbet 1999; Pritchard et al. 2000), and biotic factors such as competition, predation, cannibalism, and prey availability (Fincke 1994, 1999; Krishnaraj & Pritchard 1995; Johansson 1996; Wellborn et al. 1996; Suhling et al. 2005). Detailed ecological studies of the species discussed here, es-

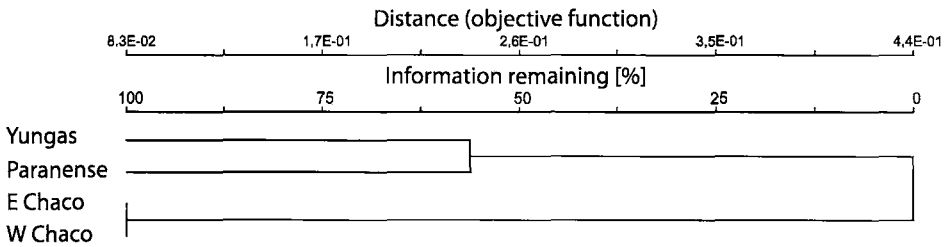


Figure 5: Dendrogram from cluster analysis (Sorensen) for odonate assemblages of Argentine Yungas and Paranense biomes and Western and Eastern Chaco sectors.

pecially of their larvae, are needed to determine the relative influence of these factors on the observed patterns.

In the Chaco most waters are ephemeral or affected by heavy floods (Prado 1993). In such heterogeneous habitats, little predictable in space and time, special-

Table 4. Indicator taxa for habitat type obtained by combining relative abundance and frequency of species within each class according to Dufrêne & Legendre's (1997) method. LM: marsh; LP: large lentic permanent, including large ponds, oxbow lakes, and dams. Indicator values range from 0 to a maximum of 100; perfect indicator: always present and only within that particular class. MC: Monte Carlo test of significance of observed maximum indicator value for taxa (with 1,000 permutations). Only taxa with a statistically significant indicator value (larger than expected by chance, $p < 0.05$) and an observed indicator value higher than 50 are shown, and taxa with a possibly meaningful 'high' value are highlighted.

Species	Habitat	Observed indicator value	MC indicator value		<i>p</i>
			Mean	s.d.	
<i>Acanthagrion cuyabae</i>	LM	63.8	24.7	13.27	0.034
<i>Argentagrion ambiguum</i>	LM	62.2	25.4	13.00	0.036
<i>Erythemis peruviana</i>	LM	77.9	22.6	12.96	0.012
<i>Erythrodiplax ochracea</i>	LM	80.5	21.8	11.95	0.008
<i>Erythrodiplax paraguayensis</i>	LM	70.6	24.5	13.52	0.023
<i>Erythrodiplax umbrata</i>	LM	57.7	27.6	12.91	0.033
<i>Micrathyria longifasciata</i>	LM	55.0	27.9	12.40	0.024
<i>Telebasis willinki</i>	LP	72.7	28.7	12.72	0.002
<i>Diastatops intensa</i>	LP	60.0	20.5	12.29	0.010
<i>Erythemis plebeja</i>	LP	69.2	24.0	13.31	0.026
<i>Miathyria marcella</i>	LP	72.7	28.5	12.85	0.002
<i>Micrathyria hesperis</i>	LP	52.7	22.3	12.94	0.031
<i>Perithemis mooma</i>	LP	58.6	27.1	13.00	0.038

Table 5. Richness and percentage complementarity of odonate assemblages from Yungas and Paranense biomes compared with Chaco biome and Chaco sectors. In brackets: number of species in common.

	Yungas	Chaco	W Chaco	E Chaco	Paranense
Species richness	105	88	72	54	190
Chaco	63.12 (52)	–	–	–	–
W Chaco	61.71 (49)	–	–	–	–
E Chaco	78.62 (28)	–	58.42 (37)	–	–
Paranense	71.74 (65)	67.98 (65)	70.29 (60)	80.39 (40)	–

ization might be less likely (Holt 1985), and communities are composed mainly of generalists (Hof et al. 2005; Suhling et al. 2003, 2006) capable of colonizing all habitat types due to their rapid development and high dispersal capabilities (Johansson & Suhling 2004; Suhling et al. 2004). By hosting generalist species, temporary environments do not offer unique species by which to identify them, which also explains the low level of endemism found for this biogeographic province. Rivers showed a low number of odonates and rendered no species of indicator value. More sampling is necessary to verify if this apparent poverty of species is real or merely a result of the low number of rivers studied. However, based on a similarly low number of localities, marshes and permanent impoundments such as oxbow lakes and dams contributed highly to the regional gamma diversity and presented some species with potential value as indicators. The indicator value of these species could be tested by further sampling in well-preserved reference localities and sites with different degrees of alteration. Absence of these indicator species may then be used to identify threatened environments and monitor the impact of human activities on the aquatic biodiversity of the area.

Distribution and biogeography

Most odonate species found in the Chaco are distributed in other biomes of the Neotropical region. From the 12 species recorded from the Chaco and absent in neighboring Yungas and Paranense biomes (Appendix), eight are distributed across other biomes in Argentina or other countries, i.e. *Aphylla dentata* occurs from Venezuela and the Guyanas S to central Argentina, *Erythemis carmelita* from Colombia and Venezuela S to Brazil, *Macrothemis heteronycha* from Venezuela south to S Brazil and Paraguay, *Micrathyria tibialis* from Panama south to Paraguay, and *Nephepeltia aequisetis* from Bolivia and SE Brazil to Paraguay. *Edonis helena* is still known only from its original description, which included two males from Paraná State in the Cerrado biome of SE Brazil (Needham 1903), and subsequent specimens from Corrientes in the Argentine Chaco (Ris 1911). *Erythrodiplax* sp. nov, 1 and *Oligoclada rubribasalis* have been found also in the Pampean

biome (von Ellenrieder & Garrison 2008; collection data at MLP). Only four species, all of them new when first found in the Chaco, can be considered as potential endemics for this biogeographical province: *Aeolagrion philipi*, known also from the Chaco in Bolivia and Paraguay (Tennessen 2009), *Orthemis philipi*, known also from the Chaco in Paraguay (von Ellenrieder 2009b), *Telebasis* sp. nov. 1 and *Telebasis* sp. nov. 2, the last two known only from females and still undescribed. According to Morrone (2001), both the Cerrado and Pampean biogeographical provinces together with Caatinga, Chaco, and Monte belong in the Chaco subregion of the Neotropical region; the distribution of *Edonis helena*, *Erythrodiplax* sp. nov. 1, and *Oligoclada rubribasalis* fits well within this sub-region. This, plus the fact that assemblages from E and W Chaco are more similar among themselves than with either Yungas or Paranense biomes shows that odonates agree well with the scheme of biogeographic provinces that was proposed based on plants, vertebrates, and other groups of invertebrates (Cabrera & Willink 1973; Morrone 2001).

Conservation

Less than half the odonate species recorded (36, representing 41%) were found within one or more surveyed protected areas (Appendix). Ecosystems within this biogeographic province are currently threatened due to ongoing expansion of cultivated areas (mostly monocultures of soy beans and pastures; Morello 1983), logging, and overgrazing (DPN 2009). Since only slightly over 1% of the Chaco is encompassed within protected areas (Buckart et al. 1994), the value of reliable indicators in determining the conservation status of freshwater habitats in this area is undeniable. Wetlands provide essential ecological services and should not be allowed to degrade; establishment of a multimetric index of biological integrity for wetlands and of regulations geared towards wetland protection have been identified as urgent (EPA 2002; RAMSAR 2007). The results of this study imply that some odonates of the Chaco could be potential indicators for natural condition of at least oxbows and lakes, and probably also of marshes. As monitoring odonates is simple and economical, they could constitute a valuable tool when selecting metrics for the development of such an index.

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Appendix. Species recorded from the Argentine Chaco — **bold**: new record for Argentina; underlined: known from examined collections and literature only; *: absent from Paranense and Yungas biomes in Argentina; L: larva described; PA: present in Protected Areas; W: Western Chaco; E: Eastern Chaco; Argentine Province within Chaco (**bold** = new record): Sa: Salta; Fo: Formosa; Ch: Chaco; SE: Santiago del Estero; Co: Corrientes; Tu: Tucumán; SF: Santa Fe; Cb: Córdoba; Habitat: LeT: small lentic temporary; LeM: marsh; LeP: large lentic permanent; Lo: lotic.

CALOPTERYGIDAE

Hetaerina rosea Selys, 1853: L, W, Sa, SE, Co, LeT, Lo

Mnesarete grisea (Ris, 1918): L, W, Sa, Tu, LeT, Lo

LESTIDAE

Lestes bipupillatus Calvert, 1909: L, W, Ch, LeT

Lestes forficula Rambur, 1842: L, W, Sa, LeT

Lestes spatula Fraser, 1946: L, W+E, Sa, **Fo**, Ch, SE, Co, LeT, LeM, LeP

COENAGRIONIDAE

Acanthagrion cuyabae Calvert, 1909: PA, W+E, **Sa**, Fo, LeT, LeM, LeP, Lo

Acanthagrion lancea Selys, 1876: W+E, Sa, **Fo**, Ch, **SE**, Co, LeT, LeP, Lo

Acanthagrion peruvianum Leonard, 1977: W, Sa, SE, LeT, LeP, Lo

Aeolagrion philipi Tennessen, 2009*: E, Fo, LeT

Argentagrion ambiguum (Ris, 1904): L, PA, W+E, Sa, Fo, Ch, Co, SF, LeT, LeM, LeP

Argia joergenseni Ris, 1913: L, W, Sa, Cb, LeT, Lo

Enallagma novaehispaniae Calvert, 1907: L, W, Sa, SE, LeP

Homeoura chelifera (Selys, 1876): L, PA, W+E, Sa, Co, LeT, LeP

Homeoura lindneri (Ris, 1928): E, Fo, Ch, Co, LeT

Ischnura capreolus (Hagen, 1861): L, PA, W+E, Sa, **Fo**, Co, Tu, LeT, LeP

Ischnura fluviatilis (Selys, 1876): L, PA, W+E, Sa, Fo, Ch, SE, Co, LeT, LeM, LeP, Lo

- Oxyagrion ablutum* Calvert, 1909: L, W, Sa, Lo
Oxyagrion rubidum (Rambur, 1842): L, W, Sa, SE, LeT
Telebasis inalata (Calvert, 1961): W, LeT
Telebasis obsoleta (Selys, 1876): W+E, **Sa**, Fo, LeT
Telebasis willinki Fraser, 1948: L, PA, W+E, Sa, Fo, Ch, Co, LeT, LeP
Telebasis* sp. nov. 1: PA, E, **Ch**, Co, LeT
Telebasis* sp. nov. 2: E, **Fo**, LeT
- AESHNIDAE
Anax amazili (Burmeister, 1839): L, W+E, Sa, Ch, SE, Co, LeT
Coryphaeschna adnexa (Hagen, 1861): L, W+E, Sa, **Fo**, Ch, Co, LeT, LeP
Coryphaeschna perrensi (McLachlan, 1887): L, E, Co, LeT
Gynacantha bifida Rambur, 1842: L, E, Co, LeT
Gynacantha convergens Förster, 1908: E, **Ch**, LeT
Rhionaeschna absoluta (Calvert, 1952): L, W, Sa, SE, Cb, LeT, LeP, Lo
Rhionaeschna bonariensis (Rambur, 1842): L, PA, W+E, Sa, Fo, Ch, SE, Co, Tu, SF, Cb, LeT, LeP
Triacanthagyna nympha (Navás, 1933): L, W, **Ch**, LeT
- GOMPHIDAE
Aphylla producta Selys, 1854: L, W, Sa, SE, Co, LeP
Aphylla dentata Selys, 1859*: PA, W, E, **Fo**, LeP
Aphylla distinguenda (Campion, 1920): PA, W, **Fo**, LeP
Epigomphus paludosus Hagen in Selys, 1854: L, W, SE, LeT
Phyllocycla argentina (Hagen in Selys, 1878): L, W+E, Sa, Co, LeT, LeP
Phyllocycla viridipleuris (Calvert, 1909): L, W, Sa, Lo
- LIBELLULIDAE
Brachymesia furcata (Hagen, 1861): L, PA, W+E, Sa, SE, Co, LeT, LeP
Brachymesia herbida (Gundlach, 1889): L, PA, W+E, **Fo**, Co, LeT, LeP
Diastatops intensa Montgomery, 1940: PA, W+E, **Sa**, Fo, Co, LeT, LeP
Dythemis multipunctata Kirby, 1894: L, W, Sa, LeT, LeP
Edonis helena Needham, 1905*: E, Co, LeT
Elasmothermis cannaerioides (Calvert, 1906): L, W, Sa, Lo
Erythemis attala (Selys, 1857): L, W+E, Sa, Fo, Ch, Co, LeT
Erythemis carmelita Williamson, 1923*: E, **Fo**, LeT
Erythemis credula (Hagen, 1861): L, PA, E, Co, LeT
Erythemis mithroides (Brauer, 1900): L, W, Fo, Ch, Co, LeT
Erythemis peruviana (Rambur, 1842): L, PA, W+E, Fo, Ch, Co, LeT, LeM, LeP
Erythemis plebeja (Burmeister, 1839): L, PA, W+E, Sa, Fo, Ch, SE, Co, LeT, LeP
Erythemis vesiculosa (Fabricius, 1775): L, PA, W+E, Sa, Fo, Ch, SE, Co, Cb, LeT, LeM, LeP
Erythrodiplax atroterminata Ris, 1911: L, W+E, Co, LeT, LeP
Erythrodiplax basalis (Kirby, 1897): W, SE, LeT, LeP
Erythrodiplax corallina (Brauer, 1865): L, W, Sa, SE, Co, LeT, LeP
Erythrodiplax fusca (Rambur, 1842): L, E, Ch, Co, LeT

- Erythrodiplax media* Borrer, 1942: W, Sa, **Fo**, LeT, LeP
Erythrodiplax melanorubra Borrer, 1942: L, W, SE, LeP
Erythrodiplax nigricans (Rambur, 1842): L, W+E, **Sa**, **Fo**, Ch, SE, Co, LeT, LeP
Erythrodiplax ochracea (Burmeister, 1839): L, PA, W+E, Fo, Ch, SE, Co, LeT, LeM, LeP
Erythrodiplax paraguayensis (Förster, 1905): L, PA, W+E, Fo, Ch, Co, LeT, LeM, Lo
Erythrodiplax umbrata (Linnaeus, 1758): L, PA, W+E, Sa, Fo, Ch, **SE**, Co, Tu, SF, LeT, LeM, LeP
Erythrodiplax sp. nov. 1*: PA, E, Co, LeT
Erythrodiplax sp. nov. 2: W, Sa, **SE**, Tu, LeT
Idiataphe longipes (Hagen, 1861): PA, E, Co, LeT
Macrothemis heteronycha (Calvert, 1909)*: E, Co, LeT
Macrothemis imitans Karsch, 1890: W+E, Sa, SE, LeT, LeP, Lo
Macrothemis inacuta Calvert, 1898: L, PA, W+E, Sa, Fo, LeT, LeP
Miathyria marcella (Selys, 1857): L, PA, W+E, Sa, Fo, Ch, SE, Co, Tu, SF, LeT, LeP
Micrathyria hesperis Ris, 1911: L, PA, W+E, Sa, **Fo**, Ch, SE, Co, LeT, LeP
Micrathyria hypodidyma Calvert, 1906: L, W+E, Sa, Fo, Ch, Co, LeT
Micrathyria longifasciata Calvert, 1909: L, PA, W+E, Sa, Fo, Ch, SE, Co, LeT, LeM, LeP
Micrathyria ocellata dentiens Calvert, 1909: L, W, Sa, LeT
Micrathyria tibialis Kirby, 1897*: L, PA, W+E, **Sa**, Fo, Co, LeT
Nephepeltia aequisetis Calvert, 1909*: PA, E, Fo, LeT, LeP
Oligoclada laetitia Ris, 1911: L, W, **Sa**, Fo, LeT, LeP
Oligoclada rubribasalis Garrison & von Ellenrieder, 2008*: PA, E, Fo, LeP
Orthemis discolor (Burmeister, 1839): W, Sa, Ch, LeT
Orthemis nodiplaga Karsch, 1891: L, PA, Sa, Fo, Ch, SE, Co, LeT, LeP
Orthemis philipi von Ellenrieder, 2009*: W, **Sa**, LeT
Pantala flavescens (Fabricius, 1798): L, W, Sa, Fo, LeT
Pantala hymenaea (Say, 1839): L, W, **SE**, LeT
Perithemis mooma Kirby, 1889: L, PA, W+E, Sa, **Fo**, SE, Co, LeT, LeP
Tauriphila argo (Hagen, 1869): L, PA, W+E, **Sa**, Co, LeT
Tauriphila risi Martin, 1896: L, PA, W+E, **Sa**, **Fo**, Ch, SE, Co, SE, Tu, SF, Cb, LeT, LeP
Tauriphila xiphea Ris, 1913: PA, W+E, **Sa**, Co, LeT
Tramea abdominalis (Rambur, 1842): W, Sa, LeT, LeP
Tramea binotata (Rambur, 1842): L, W, Sa, Co, LeT, LeP
Tramea calverti Muttkowski, 1910: L, W, **Fo**, LeT
Tramea cophysa Hagen, 1867: L, PA, W+E, Sa, Fo, SE, Co, LeT, LeP